Maclaren, J. A., Anderson, P. S. L., Barrett, P. M., & Rayfield, E. J. (2017). Herbivorous dinosaur jaw disparity and its relationship to extrinsic evolutionary drivers. *Paleobiology*, *43*(1), 15-33. https://doi.org/10.1017/pab.2016.31

Paleobiology

CAMBRIDGE UNIVERSITY PRESS

Herbivorous dinosaur disparity and its relationship to extrinsic evolutionary drivers

Journal:	*Paleobiology*
Manuscript ID	PAB-OR-2015-0084.R4
Manuscript Type:	Article
Date Submitted by the Author:	19-Jul-2016
Complete List of Authors:	MacLaren, Jamie; Universiteit Antwerpen, Faculteit Biologie Anderson, Philip; University of Illinois System, Department of Animal Biology Rayfield, Emily; University of Bristol, School of Life Sciences Barrett, Paul; Natural History Museum, Earth Sciences Department
Geographic Location:	Belgium, United Kingdom
Taxonomy:	Dinosauria, Ornithischia, Sauropoda
Analysis:	disparity, macroevolution, geometric morphometrics
Geologic Age:	Mesozoic
Topic:	paleobiology, mandibles, biomechanics

TITLE:

Herbivorous dinosaur jaw disparity and its relationship to extrinsic evolutionary drivers

Jamie A. MacLaren, Philip S. L. Anderson, Paul M. Barrett, and Emily J. Rayfield

ABSTRACT:

Morphological responses of non-mammalian herbivores to external ecological drivers have not been quantified over extended timescales. Herbivorous non-avian dinosaurs are an ideal group to test for such responses because they dominated terrestrial ecosystems for over 155 Ma and included the largest herbivores that ever existed. The radiation of dinosaurs was punctuated by several ecologically important events, including extinctions at the Triassic-Jurassic (Tr/J) and Jurassic-Cretaceous (J/K) boundaries, the decline of cycadophytes, and the origin of angiosperms, all of which may have had profound consequences for herbivore communities. Here we present the first analysis of morphological and biomechanical disparity for sauropodomorph and ornithischian dinosaurs in order to investigate patterns of jaw shape and function through time. We find that morphological and biomechanical mandibular disparity are decoupled: mandibular shape disparity follows taxonomic diversity, with a steady increase through the Mesozoic. By contrast, biomechanical disparity builds to a peak in the Late Jurassic that corresponds to increased functional variation among sauropods. The reduction in biomechanical disparity following this peak coincides with the J/K extinction, the associated loss of sauropod and stegosaur diversity, and the decline of cycadophytes. We find no specific correspondence between biomechanical disparity and the proliferation of angiosperms. Continual ecological and functional replacement of pre-existing taxa accounts for disparity patterns through much o

f the Cretaceous, with the exception of several unique groups such as psittacosaurids that are never replaced in their biomechanical or morphological profiles.

Jamie A. MacLaren, Department of Biology, Universiteit Antwerpen, Campus Drie Eiken, Universiteitsplein, Wilrijk, Antwerp, 2610, Belgium.*

Philip S. L. Anderson, Department of Animal Biology, University of Illinois at Urbana-Champaign, 515 Morrill Hall, 505 S. Goodwin Ave., Urbana, IL 61801, USA.

Paul M. Barrett, Department of Earth Sciences, The Natural History Museum, London, Cromwell Road, London, SW7 5BD, UK.

Emily J. Rayfield, School of Earth Sciences, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, UK.*

**Corresponding authors; main corresponding author: Jamie A. MacLaren, Room C1.06, Building C, Campus Drie Eiken, Universiteitsplein 1, 2610 Antwerp, Belgium*

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.c78k5

Introduction

Sauropodomorph and ornithischian dinosaurs were the foremost herbivorous terrestrial vertebrates of the Mesozoic Era in terms of species-richness, abundance, and functional diversity (Weishampel and Norman 1989; Sereno 1999; Weishampel et al. 2004; Barrett 2014). Both groups survived two extinction events - the end-Triassic mass extinction (Tr/J) and a smaller extinction at the Jurassic/Cretaceous boundary (J/K) - and persisted through several episod

es of floral turnover, including the decline of cycadophytes and the proliferation of angiosperms (Sereno 1997; Barrett and Willis 2001; Lloyd et al. 2008; Butler et al. 2009*a*). However, relatively few studies have attempted to quantity the responses of non-avian dinosaurs to these extrinsic environmental drivers.

A number of studies have investigated the ecological and evolutionary responses of dinosaurs to the Tr/J mass extinction in terms of diversity analyses, but only a handful of studies have quantified morphological disparity (Brusatte et al. 2008*a*, *b*) or the evolution of other traits across this interval (Irmis 2011; Sookias et al. 2012). These studies found that dinosaur morphospace occupation was not greatly affected by the Tr/J extinction (Brusatte et al. 2008*a*, *b*): dinosaurian disparity remained essentially unchanged across the Tr/J boundary, whereas crurotarsans became almost completely extinct (Brusatte et al. 2008*a*). With respect to dinosaurs the J/K extinction has been studied in terms of diversity analyses (e.g. Upchurch and Barrett 2005; Barrett et al. 2009; Butler et al. 2010, 2011; Upchurch et al. 2011), and the potential ecological consequences of this event have been discussed qualitatively in terms of changes to dinosaur browsing regimes and community composition (Bakker 1978; Barrett and Willis 2001; Barrett and Upchurch 2005). Possible associations between palaeobotanical turnovers and dinosaur evolution have been proposed (e.g. Bakker 1978; Weishampel and Norman 1989; Tiffney 1992; Mustoe 2007), with the suggestion that changes in the prevalent mode of dinosaur herbivory (e.g. high-browsing vs low browsing; extensive oral processing vs lack of oral processing) were reciprocally related to changes in the taxonomic and ecological composition of contemporary plant communities. In particular, it has been suggested that a decline in sauropodomorph and stegosaur abundance and diversity might be associated with a decline in cycadophyte diversity during the Early Cretaceous, and that the ecological radiation of angiosperms during the same period may have been fostered by a coincident taxonomic radiation of lo

w browsing ornithischian dinosaurs with complex jaw mechanisms (e.g., Bakker 1978; Weishampel and Norman 1989; Tiffney 1992; Mustoe 2007). Hypotheses regarding dinosaur-plant coevolution have been more recently tested quantitatively and qualitatively using spatiotemporal comparisons between the dinosaur and palaeobotanical records (Barrett and Willis 2001; Butler et al. 2009*a*, *b*, 2010). These diversity-based spatiotemporal studies found no definitive evidence for the co-radiation of any Mesozoic plant and dinosaur group, although some temporal correlations were suggestive of possible interactions. Physiological limits on some of these coevolutionary hypotheses have also been proposed on the basis of the possible nutritional value of potential food plants (e.g., Hummel et al. 2008; Gee 2011).

Disparity analyses quantify morphological diversity within a group of organisms, rather than merely documenting taxonomic richness (Wills et al. 1994; Ciampaglio et al. 2009). Unlike species richness estimates, disparity analyses can be robust to sampling biases and document the variation in morphology and potential function within taxonomic groups (Wills et al. 1994). Assessments of morphological disparity using either anatomical measurements or cladistic characters have been conducted on various extinct vertebrate groups, including dinosaurs (Brusatte et al. 2008*a*, *b*, 2012; Young and Larvan 2010; Butler et al. 2011; Foth and Rauhut 2013; Button et al. 2014). By contrast, a new method for assessing the diversity of biomechanical profiles, multivariate biomechanical disparity (Anderson 2009; Anderson et al. 2011, 2013; Stubbs et al. 2013), has not been widely applied. Biomechanical disparity offers a novel means to quantify variation in biomechanically relevant traits and to infer their potential ecological significance: for example, biomechanical traits might include mechanical advantage (the ratio of muscle moment arms indicating the efficiency of force transfer during biting), polar moment of inertia (a proxy for flexural stiffness), and mandibular articulation offset (dicting simultaneous occlusion of the entire tooth row, or scissor-like occlusion) (Anderson 200

9; Anderson et al. 2011, 2013; Stubbs et al. 2013). Other studies have explored disparity of in dividual biomechanical traits such as mechanical advantage (Sakamoto 2010; Brusatte et al. 2012), average maximum stress, or a metric of skull strength (Foth and Rauhut 2013). Continuous measurements can be projected into multivariate 'biomechanical morphospace'. Previous work in this area has used two-dimensional views of mandibular elements to investigate the appearance and diversity of biomechanical profiles during the radiation of Paleozoic fishes (Anderson 2009; Anderson et al. 2011), the water-to-land transition in tetrapods (Anderson et al. 2013), the Mesozoic diversification of crocodylomorphs (Stubbs et al. 2013), and niche partitioning in sauropod dinosaurs (Button et al. 2014).

Despite previous work, the functional responses to these potential evolutionary drivers, and hence how the organism interacted with its environment and potential drivers of selection, have not been quantified. Without this information we lack a complete picture of how dinosaur communities and clades interacted with and exploited Mesozoic environments over time. In addressing these questions, assessing the morphological variation evident from the fossil record may not be sufficient, as we do not know whether morphology and morphological diversity are reliable predictors of function and functional diversity. Therefore, in order to assess the relationship between jaw shape, function, and extrinsic evolutionary drivers, we provide the first quantitative assessment of the morphological and biomechanical disparity of an individual functional unit (the lower jaw) in herbivorous non-avian dinosaurs through time. This approach compliments previous attempts to examine these questions though spatiotemporal comparisons of species-richness patterns and provides the only rigorous biomechanically and functionally based analysis of these issues attempted to date. We hypothesise that ornithischians and sauropodomorphs will show distinct morphologies and biomechanical profiles (i.e., in both the shape and mechanical capabilities of the jaw). We also hypothesise that the shift in pl

ant community structure after the J/K boundary will trigger a corresponding shift in dinosauri an jaw biomechanical profiles, due to the differing physiognomies, digestibility, and mechani cal properties of the varied potential food plant clades that were ecologically important at diff erent times throughout the Mesozoic (Bakker 1978; Weishampel 1984; Niklas 1992; Hummel et al. 2008; Gee 2011). We use a geometric morphometric landmark analysis to compare dino saur mandibular shape variability to variation in mandibular biomechanical profiles. We then compare these data with the timing of several extrinsic events (tetrapod extinctions, changes i n floral communities) that have been proposed to influence dinosaur evolutionary history, in order to determine whether coincident patterns are present.

Materials and Methods

Data for two-dimensional landmark and biomechanical trait analyses were compiled f rom 167 sauropodomorph and ornithischian dinosaur taxa (see Supplementary Information; A ppendix 6). Herbivorous non-avian theropods were excluded from this dataset as complete m andibular material for these animals is rare. A mandibular biomechanical profile represents a good proxy for characterising the feeding system as the mandible is primarily adapted for fee ding, whereas the cranium has multiple functional roles, some of which are unrelated to feedi ng, such as housing the brain and sensory organs (Hylander et al. 1991; Hylander and Johnso n 1997).

Morphology. The archosaur mandible is a primarily planar structure, although its mor phology does differ between groups, with varying degrees of inturning and bowing, particular ly with respect to its symphyseal region (Romer 1956). However, to include as many taxa as possible, in order to account for the greatest amount of biomechanical and mandibular and de ntal shape variation, we selected a standard lateral view of the mandible as the basis for this st

udy. Two-dimensional (2D) landmarks were applied to homologous and analogous points on lateral images of dinosaur jaws using tpsDig II software (Rohlf 2004; Zelditch et al. 2012). Si x fixed landmarks were described, identifying biologically and operationally homologous poi nts on both sauropodomorph and ornithischian jaws (see Supplementary Figure S1). The over all morphology of each jaw was described by a series of sliding semi-landmarks (sLM). Six s LM curves, each bracketed by two of the fixed landmarks, were used to define the shape of th e jaw. In total, 88 landmarks (both fixed and sliding) were described. Semi-landmarks were sl id using the Chord-d^2 technique to minimise Procrustes distances rather than bending energy (Rohlf 2008); this was performed in tpsRelw. Described curves were appended to landmarks i n tpsUtil (Rohlf 2004); appended landmarks were then superimposed using generalized least squares (Procrustes) methods in tpsRelw (Rohlf 2008). Procrustes superimposition aligned ja ws, eliminating scale, location, and rotational differences between specimens (Rohlf 2004). C onsensus models, partial warps, and relative warps were then calculated using tpsRelw softwa re. Relative warp scores were subjected to principal components analysis (PCA) to produce s hape-based morphospace plots.

Biomechanics. Eighteen continuous biomechanical characters or traits were quantified , many of which have important functional consequences in extant organisms (Table 1). Full details of the biomechanical characters are described in the Supplementary Information. Bio mechanical trait measurements were standardised using a Z-transformation technique, giving all characters a mean of 0 and variance of 1 (Anderson et al. 2011). A standardised matrix of biomechanical character scores was then subjected to principal coordinates analysis (PCoA), using the Gower model to correct for missing data to produce biomechanical morphospace pl ots. PCoA and creation of morphospace plots was performed in Past v.3 (Hammer et al. 2001).

Significant differences in morphospace occupation were tested using non-parametric multivariate analysis of variance (NPMANOVA) in Past v.3 (Hammer et al. 2001). All principal axes accounting for more than 1% of variation were used in the NPMANOVA, resulting in 12 axes for shape-based and 15 axes for biomechanical morphospace. Principal axes were used to display two types of morphospace comparisons: overall shape-based and biomechanical morphospace between sauropodomorphs and ornithischians. We also created a series of morphospace plots representing eight 20 Ma time slices. These time slices were constructed by combining taxa from two adjacent 10 Ma time bins used for the disparity analyses (see below). Combining time bins allowed for good sample size and enabled comparisons across major ecological transitions e.g., mass extinction events.

Disparity. Disparity through time was calculated across sixteen 10 Ma time bins. The lengths of the time bins either side of the Tr/J boundary were adjusted to accommodate the date of the boundary as in Butler et al. (2012). Use of 10 Ma time bins enables comparisons across both the Tr/J and J/K boundaries, standardises bin length, and provides greater sample sizes per bin than those available for strict stage level comparisons. Sauropodomorph disparity was also analysed for vertical feeding envelopes in 3 m intervals. Species assignment to each maximum feeding envelope is listed in the Supplementary Information. To account for variation in the published literature, maximum sauropodomorph feeding envelopes were taken from published works, including reconstructions from new material (e.g. Upchurch and Barrett 2000; Apesteguía 2004; Sander et al. 2006; Peyer and Allain 2010; Whitlock 2011; Stevens 2013). Disparity analyses were carried out using the Morphological Disparity Analysis (MDA) package for Matlab (Navarro 2003). For all disparity tests, two variance based disparity metrics were tested: the sum of variance and mean pairwise distance. Both these metrics are robust to sample size variation (Ciampaglio et al. 2009). The sum of variance metric is plotted in the m

ain text. Mean pairwise distance results can be viewed in the Supplementary Information. Dat a were bootstrapped (1000 replicates) and 95% confidence intervals were calculated and grap hically presented. Significant differences and likelihood ratios between each time bin were ca lculated using pairwise t-tests and marginal likelihood assessment on sum of variance measur es (Finarelli and Flynn 2007). A likelihood ratio >8 is considered a likely result (Finarelli and Flynn 2007). T-test results were subsequently corrected for multiple comparisons using Bonf erroni corrections where appropriate (Holm 1979). Results for mean pairwise distance can be found in the Supplementary Information.

Results

Shape Morphospace Occupation. Our results demonstrate that sauropodomorph and o rnithischian jaws occupy significantly different regions of morphological morphospace ($p < 0.01$, Figure 1; Table 2). There is minimal overlap between sauropodomorphs and ornithischian s along PC1, with only seven ornithischian jaw morphologies occupying similar regions to sa uropodomorphs. Overlapping ornithischian taxa represent basal members of their respective g roups (basal ornithischians: *Agilisaurus* and *Pisanosaurus*; thyreophorans *Emausaurus* and *G igantspinosaurus;* and the basal ceratopsian *Yinlong*), with the exception of *Stegosaurus* (two species). Regions of overlap are occupied by a wide range of both basal and derived sauropod omorphs; these include: *Plateosaurus gracilis*, *Lamplughsaura*, mamenchisaurids, brachiosau rids, and two South American titanosaurids (*Antarctosaurus* and *Bonitasaura*). Sauropodomo rphs occupy morphospace exclusively in the –PC1 region: this region is characterised by dors oventrally narrow jaws and the lack of a prominent coronoid process. Non-eusauropod saurop odomorphs (e.g., *Plateosaurus*, *Melanonosaurus*), for the most part, account for sauropodom orph occupation of morphospace in +PC2: this region is typified by very narrow anterior jaws

213 . Macronarian and diplodocoid taxa (including *Diplodocus* and *Tapuiasaurus*) primarily occu
214 py –PC2 regions of morphospace (Figure 1). The centre of the morphospace (0.0 PC1; 0.0 PC
215 2) is occupied by non-hadrosaurid iguanodontians (*Parksosaurus*, *Theiophytalia*, and *Dryosa*
216 *urus*). Jaws in this region exhibit a greater gap between landmarks 1 and 2 than in sauropodo
217 morph morphospace (due to the presence of the predentary in iguanodontians). Disparate gro
218 ups of non-thyreophoran ornithischians expand morphospace occupation into +PC1 and +PC
219 2 (hadrosaurids) and –PC2 regions (leptoceratopsids and psittacosaurids). +PC1 and +PC2 re
220 gions typically contain jaws with prominent coronoid processes and downwardly deflected pr
221 edentaries; –PC2 regions contain robust, dorsoventrally broad jaws. Non-ceratopsid marginoc
222 ephalian jaw morphologies, such as those of psittacosaurids and leptoceratopsids, contribute s
223 trongly to the expansion of ornithischian shape morphospace, predominantly into +PC1/–PC2
224 . Taxa are absent in a region of morphospace around +0.05 PC1/ -0.075 PC2.

225 *Biomechanical Morphospace Occupation*. Our results demonstrate that sauropodomor
226 ph and ornithischian taxa also occupy significantly different regions of biomechanical morph
227 ospace ($p < 0.01$, Figures 2–3; Table 2). There is greater overlap in biomechanical morphospa
228 ce occupation than shape morphospace, with 16–20 ornithischian taxa occupying morphospac
229 e that is shared with sauropodomorphs (Figures 2–3). Overlapping ornithischian taxa include
230 basal ornithischians (*Pisanosaurus*, heterodontosaurids) and basal members of Thyreophora (
231 *Emausaurus*, stegosaurs), Marginocephalia (*Yinlong*), and Ornithopoda (*Changchunsaurus*,
232 *Dysalotosaurus*). Sauropodomorphs occupy regions of +PCo1. Non-eusauropod sauropodom
233 orphs (e.g., *Coloradisaurus*, *Pantydraco*) predominate in +PCo1/–PCo2. This region is chara
234 cterised by jaws with a high mechanical advantage and large adductor muscle attachment are
235 a. Diplodocids, non-neosauropods, and non-titanosaurian macronarians (e.g., *Mamenchisauru*
236 *s*, *Camarasaurus*) stretch sauropodomorph occupation into +PCo2. Jaws in this region also di

237 splay high mechanical advantages, coupled with high aspect ratios. Many iguanodontian, cera
238 topsid, and psittacosaurid jaw profiles occupy similar regions of +PCo2 biomechanical morp
239 hospace (Figure 2). Occupation is spread deeper into –PCo1 by leptoceratopsids (e.g., *Monta*
240 *noceratops*). This region of functional space is characterised by deep jaws with short adducto
241 r muscle attachment and a high posterior mechanical advantage. Expansion into –PCo2 is acc
242 ounted for by deep-jawed ankylosaurs (*Euoplocephalus*, *Silvisaurus*), with low tooth:jaw dept
243 h ratios and high relative dental length (Figure 2). Similar patterns are observed in PCo3, wit
244 h more basal sauropodomorphs occupying –PCo3, with a large cluster of iguanodontians and
245 ceratopsids occupying regions of central morphospace (0.0 PCo1; 0.0 PCo3). Functional load
246 ings, interpretations for the first four principal axes, and individual species placement in morp
247 hospace can be found in the Supplementary Information.

248 *Morphospace Occupation through Time*. Breakdown of shape and biomechanical mor
249 phospace into 20 Ma time bins highlights patterns of morphospace occupation by each clade t
250 hrough time (Figures 4–6). Initial occupation during the Late Triassic–Middle Jurassic is dom
251 inated by sauropodomorphs, with low numbers of contemporaneous basal ornithischians (e.g.
252 , heterodontosaurids and thyreophorans). Thyreophorans, ornithopods, marginocephalians, an
253 d heterodontosaurids all occupy similar regions of shape morphospace in the 20 Ma bin prior
254 to the J/K boundary (145–165 Ma), yet at this time, the same clades occupy disparate regions
255 of biomechanical morphospace with little overlap (Figures 5–6; 145–165 Ma, Table 3). Sauro
256 podomorphs at this time show significantly different biomechanical occupation to stegosaurs
257 and ornithopods, but not heterodontosaurids or the basal ceratopsian *Yinlong* (NPMANOVA,
258 $p<0.01$; Table 3). The sauropodomorphs are biomechanically diverse prior to the J/K boundar
259 y, occupying the region of morphospace that correlates to high tooth height:base, high mecha
260 nical advantages, and large mandibular fenestrae. After the J/K boundary, morphospace and b

iomechanical morphospace plots show a drop in sauropodomorph morphological and biomec hanical variation as sample size diminishes, and expansion in disparity by marginocephalians and, later, ornithopods (Figures 4–6; 65–145 Ma). By the Early Cretaceous, the surviving Jur assic herbivorous dinosaur clades (sauropodomorphs, marginocephalians, ornithopods, and th yreophorans) are statistically distinct in both shape and biomechanical morphospace (Table 2). Sauropodomorphs display substantially reduced variation, whereas ankylosaurs, ceratopsia ns, and ornithopods expand into hitherto unoccupied regions of biomechanical morphospace. Marginocephalians (e.g., *Psittacosaurus*) share areas of biomechanical morphospace with igu anodontians, but occupy very different regions of shape space (Figure 4; 145–105 Ma).

In the latest Cretaceous, the four clades present occupy distinct regions of shape mor phospace ($p<0.01$; Table 2), with the exception of one marginocephalian taxon (*Stegoceras*) t hat plots between non-hadrosaurid ornithopods and ankylosaurians (Figure 4; 65–85 Ma). Bio mechanically, *Stegoceras* is nested among ornithopods, and is closer to sauropods than many contemporaneous ceratopsians. Corresponding biomechanical morphospace plots show a ver y different trend. Marginocephalians overlap with both ornithopods and thyreophorans. Thyre ophorans and ornithopods do not overlap, and sauropodomorphs overlap minimally with ornit hopods (Figures 5–6; 65–85 Ma). Whereas variation in marginocephalian jaw shape and bio mechanics increases throughout the Cretaceous, ornithopod shape and biomechanical variatio n remains constant throughout the Late Cretaceous. Leptoceratopsids (e.g., *Udanoceratops*, *Montanoceratops*) extend biomechanical morphospace occupation into the region of morphos pace characterised by deep mandibles with short adductor muscle attachment and high posteri or mechanical advantages (Figure 5–6). Full details of the biomechanical character loadings a re described in the Supplementary Information (Appendix 5).

Disparity. Morphological (shape) and biomechanical disparity measures are decouple

d through the Mesozoic (Figure 7). Morphological disparity primarily tracks sample diversity (Figure 7a): it does not fluctuate greatly through the first 80 Ma of dinosaur evolution, begins to increase from the Middle Jurassic onwards, and reaches a peak in the Late Cretaceous (Fig ure 7a). There are no significant differences in disparity between time bins ($p>0.05$). By contr ast, biomechanical disparity undulates through the Mesozoic (Figure 7b), a decoupling from s ample diversity and morphological diversity. Several small peaks and troughs (for example th e peak in the Late Jurassic) correspond to increased sample size (Figure 7b, blue data points): however, time periods with greatest sample sizes do not correspond to peaks in biomechanica l disparity (during the latest Cretaceous, for example). The peak in the latest Jurassic also corr esponds with the presence of high-browsing sauropodomorphs (>9 m), which display a highe r degree of biomechanical disparity than some lower-browsing forms ($p>0.05$, see Supplemen tary Figure 10). There are no significant differences in disparity between successive time bins for either biomechanical or morphological disparity curves (at $p = 0.05$) and no marginal likel ihood values exceed the threshold value of 8. There are a few instances where disparity diver ges markedly from sample size, suggesting that a trend, albeit non-significant, might be obser ved. For example, morphological disparity rises in the Early Cretaceous, immediately after th e J/K extinction, and in the early Late Cretaceous, while sample size drops. Likewise, biomec hanical disparity drops in the Middle Jurassic whilst sample size rises slightly. Conversely, in the latest Cretaceous, sample size rises sharply whilst biomechanical disparity drops very slig htly.

Discussion

Impact of Extinction on Herbivorous Dinosaur Disparity. Our results from both morphological and biomechanical disparity curves support conclusions from previous studies

examining dinosaur disparity around extinction events (Brusatte et al. 2008*a*, 2012). Morphological disparity across the Tr/J boundary increases slightly, likely triggered by the addition of heterodontosaurid jaw profiles to the morphospace (Figure 7a). Biomechanical disparity decreases from an initial peak in the Carnian (225 Ma) to the Tr/J boundary, across which there is a further non-significant decrease (Figure 7b). The placement of taxa in biomechanical morphospace suggests that both ornithischian and sauropodomorph taxa share similar biomechanical profiles immediately before and after the Tr/J boundary (Figures 5–6). By contrast the transition across the J/K boundary shows a decoupled relationship between biomechanical and morphological disparity (Figure 7). Morphological disparity after the J/K boundary increases sharply: this pattern can be attributed to the presence of novel jaw morphologies such as those of psittacosaurids and early hadrosauroids in combination with those of new sauropod clades (Figure 4; 125–145 Ma). It should be noted that this disparity increase is non-significant, likely due to the low taxon count (n = 5). The lack of numerous dinosaur-bearing formations between the Berriasian and Albian may partially account for the low species-richness observed in this interval although it could also be attributed to the J/K extinction event (Barrett et al. 2009; Upchurch et al. 2011). Nevertheless, shape variation at this time does not track sample diversity. Biomechanical disparity shows a decrease across the J/K boundary (Figure 7b). The majority of the biomechanical profiles exhibited prior to the J/K boundary do not persist into the earliest Cretaceous (Figures 5–6; 125–145 Ma), which is consistent with the fundamental faunal turnover that takes place and the proliferation of marginocephalian and ornithopod taxa (e.g., Bakker 1978; Weishampel & Norman 1989; Barrett & Willis 2001). Finally, our results concur with disparity patterns observed in the latest Cretaceous leading to the K/Pg mass extinction (Brusatte et al. 2012): both morphological and biomechanical curves show a decrease in disparity from the Campanian to the Maastrichtian, despite a notable increase in sample size.

334

335 *Patterns of Morphospace Occupation*. Discrete morphospace occupation suggests
336 that, when considered as a single dataset, the jaws of sauropodomorphs and ornithischians are
337 different in both shape and in jaw biomechanics (Figures 1–3). Individual occupation of
338 morphospace by each taxon is graphically represented in Supplementary Figures S2–S6.
339 Limited overlap between these clades suggests little competition between ornithischians and
340 sauropodomorphs in feeding function, particularly during the latter part of the Mesozoic (see
341 also Barrett & Upchurch 2005). However, where overlap does occur it tends to be between
342 the basal members of various ornithischian clades (e.g., heterodontosaurids, basal
343 thyreophorans, and basal ceratopsians) and sauropodomorphs. This suggests that early
344 ornithischians adopted similar morphological and mechanical attributes to their feeding
345 apparatus as macronarian sauropodomorphs (Supplementary Figure 2a–c). Later groups of
346 ornithischians radiated into distinct areas of morphospace (Figures 4–6). Breakdown of
347 morphological and biomechanical morphospace into 20 Ma time bins shows that earlier
348 sauropodomorphs are, in general, replaced in their biomechanical profiles by later
349 sauropodomorphs through the Jurassic and Cretaceous (Figures 4–6). Sauropodomorph
350 morphospace occupation shows a degree of migration through time, with basal
351 sauropodomorphs occupying different regions of morphospace to Jurassic and Cretaceous
352 neosauropods (Figures 4–6; filled circles).Some later sauropods show convergence in
353 biomechanical profile with other, earlier forms. For example, the macronarian *Camarasaurus*
354 occupies very similar regions of morphospace to the earlier diverging eusauropod
355 *Datousaurus* (Supplementary Figure 2a–c), despite the former existing around 10 Ma earlier:
356 this pattern supports the results of another recent quantitative craniodental study (Button et al.
357 2014). Similarly, the titanosaurid *Antarctosaurus* occupies almost identical biomechanical

morphospace to the basal macronarian *Abrosaurus* (Supplementary Figure 2a–c). Perhaps surprisingly, we find minimal convergent occupation in biomechanical morphospace between titanosaurids (e.g. *Antarctosaurus*) and diplodocids (e.g. *Diplodocus*) (Supplementary Figure 2a–c: see also Button et al. 2014). This pattern is in contrast to shape-based morphospace (this study), in which these groups occupy similar regions of morphospace (Figures 1 and S2). Both shape-based and biomechanical morphospace patterns show extensive overlap between phylogenetically separate groups of sauropodomorphs. Within the sauropods, brachiosaurids are found to be biomechanically intermediate between basal macronarian sauropods with short snouts and closely packed tooth rows (such as *Camarasaurus*) and titanosaurids with longer snouts and pencil-like teeth (such as *Antarctosaurus*), and diplodocids are outliers in this biomechanical morphospace. This pattern supports quantitative work on sauropodomorph cranial morphology related to feeding, with similar placement of the same taxa in cranial (Button et al. 2014) and mandibular morphospace (this study). Late Jurassic sauropods such as *Camarasaurus* show some morphological overlap in mandibular shape with stegosaurs. By contrast, these same clades show minimal overlap in biomechanical morphospace: only *Gigantspinosaurus* (Stegosauria) and *Manidens* (Heterodontosauridae) share occupation of Late Jurassic sauropodomorph biomechanical morphospace (Supplementary Figures S3b–c & S4b–c). This suggests that mandibles with similar gross morphology were biomechanically and functionally differentiated by this time. In general, sauropodomorphs and heterodontosaurids occupy similar regions of both shape-based and biomechanical morphospace, and do not extend their occupation of morphospace beyond regions already occupied by the end of the Early Jurassic (Figures 4-6). From the Middle Jurassic onward, there is slight expansion of morphospace along PC1 by diplodocoid sauropodomorphs and Jurassic ornithopods (e.g., *Camptosaurus*), which is also reflected in the morphological disparity curve (Figure 4, 145–165 Ma; Figure 7a). Morphological

disparity shows an increase from the latest Jurassic through the Cretaceous with the evolution of new groups of ornithischian dinosaurs, particularly marginocephalians.

Early Cretaceous marginocephalians (psittacosaurids, *Archaeoceratops*, and *Liaoceratops*) occupy novel regions of morphological and biomechanical morphospace: these taxa share regions of biomechanical morphospace with hadrosauroids until the disappearance of basal marginocephalians prior to the last 20 Ma of the Mesozoic (Figures 4–6; 65–85 Ma). Regions of biomechanical morphospace formerly occupied by psittacosaurids were then occupied exclusively by derived hadrosaurids and ankylosaurs (Figures 5–6; 65–85 Ma). However, the morphological profile of psittacosaurids was never replaced. The latest Cretaceous sees an expansion of biomechanical and shape-based morphospace by two distinct groups of marginocephalians: ceratopsids (e.g., *Triceratops*) and leptoceratopsids (e.g., *Udanoceratops*). The biomechanical profiles of ceratopsids show no overlap with those of hadrosaurids. This supports the conclusions of Mallon and Anderson (2013) who, in their study of herbivores from the Dinosaur Park Formation (Campanian), found that contemporaneous hadrosaurids, ankylosaurs, and ceratopsids occupied different feeding niches based upon differing cranial and mandibular mechanics and morphologies. This study also supports previous conclusions on niche partitioning between hadrosaurs and ceratopsids (Mallon and Anderson 2013). However, this study also found that the majority of derived ceratopsids plot in similar regions of biomechanical morphospace to contemporaneous ankylosaurs, in contrast to the conclusions of Mallon and Anderson (2013). In addition, Asian ankylosaurs show biomechanical morphospace occupation more similar to leptoceratopsids than to ceratopsids or North American ankylosaurs. It should be noted, however, that neither leptoceratopsids nor Asian ankylosaurs were included in Mallon and Anderson (2013), which focussed solely on the Dinosaur Park Formation fauna. Leptoceratopsids expand into regions

of shape-based and biomechanical morphospace that had no previous occupants: their extreme mandibular morphologies account for the peak in morphological disparity in the latest Cretaceous (Figure 7a). Contemporaneous taxa include ceratopsids and ankylosaurs that have similar biomechanical profiles to each other (see above). This biomechanical similarity would cause disparity to be low: however, the inclusion of the highly disparate leptoceratopsids (in addition to hadrosaurids and the rhabdodontid *Zalmoxes*) leads to an increase in biomechanical disparity levels from the early Late Cretaceous. Marginocephalian, ornithopod, and thyreophoran biomechanical morphospace occupation in the latest Cretaceous suggests that these groups, whilst varying from each other in mandibular shape, also share a variety of functional and biomechanical traits relating to feeding. Late Cretaceous hadrosaurids and ankylosaurids filled the biomechanical roles vacated by Early Cretaceous non-hadrosaurid iguanodontians and nodosaurids respectively. Individual occupation of morphospace by each taxon can be viewed in Supplementary Figures S2–S6.

Dinosaur–Plant Co-evolution. Changes in dinosaur communities and feeding regimes during the Late Jurassic–Early Cretaceous interval have been linked to several major floristic changes (decline of cycadophytes, gymnosperms, and pteridophytes; rise of angiosperms to e cological dominance) (e.g., Weishampel and Norman 1989; Tiffney 1992; Mustoe 2007). Our results provide quantitative evidence that the mandibles of sauropodomorphs and ornithischia ns evolved different morphologies and biomechanical profiles, potentially enabling them to fe ed on different plants in different ways. Moreover, their minimal overlap in biomechanical m orphospace suggests that there was limited competition between ornithischians and sauropod omorphs when feeding (see also Barrett and Upchurch 2005). Our data demonstrate that there was no significant increase in the biomechanical disparity of the feeding apparatus of either

major herbivorous dinosaur clade that was coincident with the proliferation of angiosperms (Figure 7). Nevertheless, although this novel food source appears to have had no discernible i mpact on the mandibular biomechanical morphospace occupation of herbivorous dinosaurs, p atterns of morphological disparity do show a marked increase coincident with the later Cretac eous proliferation of angiosperms. This coincident increase is not interpreted as indication of direct causality, but reflects the appearance of the highly disparate ankylosaurid and leptocera topsian jaw morphotypes.

Potential links to cycadophyte decline through the Late Jurassic–Early Cretaceous are less clear. The Early Cretaceous decline in cycadophytes occurred at a time of major faunal c hange affecting dinosaur clades, but previous analyses of dinosaur and plant distribution have shown that few of the observed changes in dinosaur faunas could be linked directly with cyca dophyte decline (Butler et al. 2009*a*). Although reduced biomechanical mandibular disparity across the J/K boundary does coincide with the onset of this event, direct evidence of dinosau r herbivory on cycads is sparse (Hummel et al. 2008; Butler et al. 2009*a*; Gee 2011) and other causes relating to the poorly understood J/K extinction may also be involved (Butler et al. 20 11; Upchurch et al. 2011). In addition, morphological disparity after this extinction event sho ws a notable increase, with different clades of dinosaurs diversifying into new, unexplored re gions of mandibular morphospace (e.g., psittacosaurids, early titanosaurs). Results from this s tudy do not support a co-evolutionary relationship between herbivorous dinosaur mandibular disparity and angiosperm proliferation, and show a similarly negative relationship to the decli ne of cycadophytes. Rather, patterns of mandibular shape and mechanical diversity seem to b e most greatly affected by the extinction and emergence of different dinosaurian clades.

Sampling Issues. When disparity tracks sample diversity closely, as it does in this study for shape-based disparity, sampling bias cannot be ruled out. Morphological disparity in this study partly tracks jaw sample size, suggesting a potential bias in the dataset for some features of the disparity curve (e.g., high sample and disparity in latest Cretaceous; Figure 7a). The use of the sum of variance disparity measure and bootstrapping the data has accounted for sample size as best as is possible for the dataset (Foote 1992, 1994; Ciampaglio et al. 2009) (Figure 7a). Peaks of high shape disparity in the earliest Cretaceous and early Late Cretaceous do not correlate with peaks in sample size. Biomechanical variation displays a different trend, demonstrating a decoupling of morphological and biomechanical diversity through time. A peak in biomechanical disparity in the Late Jurassic is coincident with an increase in jaw sample size, but also corresponds to the evolution of high-browsing (>9 m) sauropods (e.g., Upchurch and Barrett 2000). In addition, many of the sauropod taxa in this time slice are recovered from the Morrison Formation of the western USA (n = 6 out of a total of 14 sauropods). The exclusion of the Morrison taxa removes the Late Jurassic peak in biomechanical disparity (Supplementary Figure 8i). A similar jack-knifing of the taxa from the Dashanpu Formation (including the 'Upper and Lower Shaximiao' formations) yielded a trough in disparity in the Middle Jurassic but retained a strong peak in the latest Jurassic (Supplementary Figure 8ii). These results suggest that the data may be sensitive to the inclusion or exclusion of particularly rich fossil-bearing sites. In addition, the lack of available jaw material from North and South American titanosaurs seriously underrepresents sauropodomorph diversity in the Cretaceous. The addition of titanosaurid taxa to the analysis may increase both the disparity and overall morphospace occupation of sauropodomorphs, although the titanosaur jaws sampled in this study already account for a broad range of morphologies (Supplementary Figure 2a–c; taxon 37–44).

Supplementary analyses of biomechanical and shape-based disparity within sauropodomorphs in relation to maximum feeding height show higher levels of disparity in high-browsing sauropods (>9 m; e.g., *Brachiosaurus*, *Mamenchisaurus*) when compared to mid-browsing taxa (6-9 m; e.g., *Camarasaurus*), and almost equal in disparity to very low-browsing sauropodomorphs (0–3 m; e.g., *Pantydraco*, *Riojasaurus*) (see Supplementary Figure 10). This pattern contrasts with sample diversity, with the lowest sample size found in the high-browsing feeding envelope (n = 6) (Supplementary Figure 10). Unfortunately, low sample sizes within each feeding level prevent any significant differences or definitive conclusions to be made. However, this pattern remains intriguing and the addition of more mandibular remains from high- and mid-browsing taxa to our sample (as and when they are discovered) would complement this study. This is an avenue of study that requires more investigation in the future to enable deeper insights into niche partitioning between sauropod groups based on maximum browse height.

Relatively few Early Cretaceous sauropodomorph, thyreophoran, or marginocephalian taxa possess well-preserved mandibular material (see list of taxa in Supplementary Information). The dip in biomechanical disparity after the J/K recovered by our analyses may, therefore, be an artefact due to either geological biases or uneven collection effort, underrepresenting the true diversity of jaw biomechanical profiles at this time. Due to the lack of complete mandibles from rebbachisaurids, dicraeosaurids, and other clades, it is possible that the latest Jurassic and earliest Cretaceous disparity levels reported herein are currently under-sampling the total diversity of mandible morphology and potential function. Such exclusions cannot be corrected for by our analyses, and represent a limitation of the fossil material currently available.

Conclusions

For the first time we have quantified the morphological and biomechanical variation of ornithischian and sauropodomorph jaws throughout the Mesozoic, and examined how diversity related to external extrinsic drivers such as extinction events and the rise of angiosperms. We find that herbivorous dinosaur clades have jaws that occupy different regions of morphospace throughout the Mesozoic. Furthermore, sauropodomorphs and ornithischians have jaws that also function in broadly different ways, yet there is some potentially convergent overlap in biomechanical function between different ornithischian clades in the Cretaceous. Basal members of each clade tend to be more similar in form and function to each other whilst derived taxa are more functionally and morphologically divergent. Herbivorous dinosaur jaws maintained a numerically steady diversity of biomechanical traits, with a peak observed in the Late Jurassic triggered by the diversification of high browsing sauropods. This is consistent with a rapid evolutionary radiation in biomechanical diversity among herbivorous dinosaurs followed by a plateau. The Tr/J extinction had no overall effect on biomechanical variation among herbivorous dinosaurs, despite fundamental changes in floral and faunal composition across the boundary. This consistency suggests that Early Jurassic dinosaurs filled the functional feeding niches vacated by the extinction of Late Triassic taxa. Similar successive replacement patterns are also seen in Devonian gnathostomes and Devonian to mid-Pennsylvanian tetrapodomorphs (Anderson et al. 2011, 2013). Biomechanical disparity across the J/K boundary suggests that large-scale faunal turnover at this time did affect mandibular disparity, which did not recover to pre-J/K disparity levels through the Cretaceous (Figure 7). A diverse fauna of high-browsing sauropods did not persist into the Early Cretaceous, and the sauropodomorph contribution to overall disparity wanes through the Cretaceous, despite a later increase in their Late Cretaceous species-richness. The highly specialised psittacosaurids were not replaced in their bi

omechanical profile. However, their role as a biomechanically disparate group in Asia is later filled by Late Cretaceous leptoceratopsids (e.g., *Udanoceratops*), a group that is also present i n North America. Late Cretaceous hadrosaurids and ankylosaurids filled the biomechanical ro les vacated by Early Cretaceous non-hadrosaurid iguanodontians and nodosaurids respectivel y. Our results imply that, after the establishment of peak overall biomechanical variation in th e latest Jurassic, only marginocephalians demonstrated widespread variation in biomechanica l profiles over time, triggered by the isolated adaptive radiations of psittacosaurids and leptoc eratopsians. The remainder of Cretaceous herbivorous dinosaurs underwent progressive niche replacement, with successive replacement by related taxa with comparable biomechanical pro files.

Acknowledgements

The authors would like to thank D. Button and T. Stubbs (both University of Bristol) for taxonomic and methodological discussion, and S. Chapman (NHM) for specimen provision. Funding support was received from the Bob Savage Fund of University of Bristol, and from a BBSRC grant BB/I011668/1 awarded to EJR. Helpful reviews of this contribution were received from J. Whitlock and an anonymous referee.

References

Anderson, P. S. L. 2009. Biomechanics, functional patterns, and disparity in Late Devonian arthrodires. Paleobiology 35:321–342.

Anderson, P. S. L., M. Friedman, and M. Ruta. 2013. Late to the table: diversification of tetrapod mandibular biomechanics lagged behind the evolution of terrestriality.

549 Integrative and Comparative Biology 53:197–208.

550 Anderson, P. S. L., M. Friedman, M. D. Brazeau, and E. J. Rayfield. 2011. Initial radiation of
551 jaws demonstrated stability despite faunal and environmental change. Nature 476:206–
552 209.

553 Apesteguía, S. 2004. *Bonitasaura salgadoi* gen. et sp. nov.: a beaked sauropod from the Late
554 Cretaceous of Patagonia. Naturwissenschaften 91:493–497.

555 Bakker, R. T. 1978. Dinosaur feeding behaviour and the origin of flowering plants. Nature
556 274:661–663.

557 Barrett, P. M. 2014. Paleobiology of herbivorous dinosaurs. Annual Review of Earth and
558 Planetary Sciences 42:207–230.

559 Barrett, P. M., and K. J. Willis. 2001. Did dinosaurs invent flowers? Dinosaur–angiosperm
560 coevolution revisited. Biological Reviews 76:411–447.

561 Barrett, P. M., and P. M. Upchurch. 2005. Sauropodomorph diversity through time. Pp.125–
562 128 *in* K. A. Curry Rogers and J. A. Wilson, eds. The Sauropods: Evolution and
563 Paleobiology. University of California Press, Berkeley.

564 Barrett, P. M., A. J. McGowan, and V. Page. 2009. Dinosaur diversity and the rock record.
565 Proceedings of the Royal Society B 276:2667–2674.

566 Brusatte, S. L., M. J. Benton, M. Ruta, and G. T. Lloyd. 2008a. The first 50 Myr of dinosaur
567 evolution: macroevolutionary pattern and morphological disparity. Biology Letters
568 4:733–736.

569 ——— 2008b. Superiority, competition, and opportunism in the evolutionary radiation of
570 dinosaurs. Science 321:1485–1488.

571 Brusatte, S. L., R. J. Butler, A. Prieto-Márquez, and M. A. Norell. 2012. Dinosaur

572 morphological diversity and the end-Cretaceous extinction. Nature Communications
573 3:804.

574 Butler, R. J., P. M. Barrett, P. Kenrick, and M. G. Penn. 2009a. Testing co-evolutionary
575 hypotheses over geological timescales: interactions between Mesozoic non-avian
576 dinosaurs and cycads. Biological Reviews 84:73–89.

577 Butler, R. J., P. M. Barrett, P. Kenrick, and M. G. Penn. 2009b. Diversity patterns amongst
578 herbivorous dinosaurs and plants during the Cretaceous: implications for hypotheses of
579 dinosaur/angiosperm co-evolution. Journal of Evolutionary Biology 22:446–459.

580 Butler, R. J., P. M. Barrett, M. G. Penn, and P. Kenrick. 2010. Testing coevolutionary
581 hypotheses over geological timescales: interactions between Cretaceous dinosaurs and
582 plants. Biological Journal of the Linnean Society 100:1–15.

583 Butler, R. J., S. L. Brusatte, B. Andres, and R. B. J. Benson. 2012. How do geological
584 sampling biases affect studies of morphological evolution in deep time? A case study of
585 pterosaur (Reptilia: Archosauria) disparity. Evolution 66:147–162.

586 Butler, R. J., R. B. J. Benson, M. T. Carrano, P. D. Mannion, and P. Upchurch. 2011. Sea
587 level, dinosaur diversity and sampling biases: investigating the “common cause”
588 hypothesis in the terrestrial realm. Proceedings of the Royal Society B 278:1165–1170.

589 Button, D. J., E. J. Rayfield, and P. M. Barrett. 2014. Cranial biomechanics underpins high
590 sauropod diversity in resource-poor environments. Proceedings of the Royal Society B
591 281:20142114.

592 Ciampaglio, C. N., M. Kemp, and D. W. McShea. 2009. Detecting changes in morphospace
593 occupation patterns in the fossil record: characterization and analysis of measures of
594 disparity. Paleobiology 27:695–715.

595 Finarelli, J. A., and J. J. Flynn. 2007. The evolution of encephalization in caniform
596 carnivorans. Evolution; international journal of organic evolution 61:1758–1772.

597 Foote, M. 1992. Rarefaction analysis of morphological and taxonomic diversity.
598 Paleobiology 18:1–16.

599 ——— 1994. Morphological disparity in Ordovician-Devonian Crinoids and the Early
600 Saturation of Morphological Space. Paleobiology 20:320–344.

601 Foth, C., and O. W. M. Rauhut. 2013. The good, the bad, and the ugly: The Influence of skull
602 reconstructions and intraspecific variability in studies of cranial morphometrics in
603 theropods and basal saurischians. PLoS One 8:e72007.

604 Gee, C. T. 2011. Dietary options for the sauropod dinosaurs from an integrated botanical and
605 paleobotanical perspective. Pp.34–56 *in* N. Klein, K. Remes, C. T. Gee, and P. M.
606 Sander, eds. Biology of the Sauropod Dinosaurs: Understanding the Life of Giants.
607 Indiana University Press, Indianapolis.

608 Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. Paleontological statistics software
609 package for education and data analysis. Palaeontologia Electronica 4:9.

610 Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal
611 of Statistics 6:65–70.

612 Hummel, J., C. T. Gee, K.-H. Südekum, P. M. Sander, G. Nogge, and M. Clauss. 2008. In
613 vitro digestibility of fern and gymnosperm foliage: implications for sauropod feeding
614 ecology and diet selection. Proceedings of the Royal Society B 275:1015–1021.

615 Hylander, W. L., and K. R. Johnson. 1997. In vivo bone strain patterns in the zygomatic arch
616 of macaques and the significance of these patterns for functional interpretations of
617 craniofacial form. American Journal of Physical Anthropology 102:203–232.

618 Hylander, W. L., P. G. Picq, and K. R. Johnson. 1991. Masticatory-stress hypotheses and the
619 supraorbital region of primates. American Journal of Physical Anthropology 86:1–36.

620 Irmis, R. B. 2011. Evaluating hypotheses for the early diversification of dinosaurs. Earth and
621 Environmental Science Transactions of the Royal Society of Edinburgh 101:397–426.

622 Lloyd, G. T., K. E. Davis, D. Pisani, J. E. Tarver, M. Ruta, M. Sakamoto, D. W. E. Hone, R.
623 Jennings, and M. J. Benton. 2008. Dinosaurs and the Cretaceous Terrestrial Revolution.
624 Proceedings of the Royal Society B 275:2483–2490.

625 Mustoe, G. 2007. Coevolution of cycads and dinosaurs. Cycad Newsletter 30:6–9.

626 Navarro, N. 2003. MDA: a MATLAB-based program for morphospace-disparity analysis.
627 Computers & Geosciences 29:655–664.

628 Peyer, K., and R. Allain. 2010. A reconstruction of *Tazoudasaurus naimi* (Dinosauria,
629 Sauropoda) from the late Early Jurassic of Morocco. Historical Biology 22:134–141.

630 Rohlf, F. J. 2004. *tpsDig*. Department of Ecology and Evolution, State University of New
631 York, Stony Brook, New York.

632 ——— 2008. *tpsRelW*. Department of Ecology and Evolution, State University of New York,
633 Stony Brook, New York.

634 Sander, P. M., O. Mateus, T. Laven, and N. Knótschke. 2006. Bone histology indicates
635 insular dwarfism in a new Late Jurassic sauropod dinosaur. Nature 441:739–741.

636 Sereno, P. C. 1997. The origin and evolution of dinosaurs. Annual Review of Earth and
637 Planetary Sciences 25:435–489.

638 ——— 1999. The evolution of dinosaurs. Science 284:2137–2147.

639 Sookias, R. B., R. J. Butler, and R. B. J. Benson. 2012. Rise of dinosaurs reveals major body-
640 size transitions are driven by passive processes of trait evolution. Proceedings of the

641 Royal Society B 279:2180–2187.

642 Stevens, K. A. 2013. The articulation of sauropod necks: methodology and mythology. PloS
643 one 8:e78572.

644 Stubbs, T. L., S. E. Pierce, E. J. Rayfield, and P. S. L. Anderson. 2013. Morphological and
645 biomechanical disparity of crocodile-line archosaurs following the end-Triassic
646 extinction. Proceedings of the Royal Society B 280:20131940.

647 Tiffney, B. H. 1992. The role of vertebrate herbivory in the evolution of land plants.
648 Palaeobotanist 41:87–97.

649 Upchurch, P. M., and P. M. Barrett. 2000. The evolution of sauropod feeding mechanisms.
650 Pp.79–122 *in* H.-D. Sues, ed. Evolution of Herbivory in Terrestrial Vertebrates:
651 Perspectives from the Fossil Record. Cambridge University Press, Cambridge.

652 ——— 2005. Phylogenetic and taxic perspectives on sauropod diversity. Pp.104–124 *in* K.
653 A. Curry Rogers and J. A. Wilson, eds. The Sauropods: Evolution and Paleobiology.
654 University of California Press, Berkeley.

655 Upchurch, P. M., P. D. Mannion, R. B. J. Benson, R. J. Butler, and M. T. Carrano. 2011.
656 Geological and anthropogenic controls on the sampling of the terrestrial fossil record: a
657 case study from the Dinosauria. Geological Society, London, Special Publications
658 358:209–240.

659 Weishampel, D. B., and D. B. Norman. 1989. Vertebrate herbivory in the Mesozoic; jaws,
660 plants, and evolutionary metrics. Geological Society of America Special Papers 238:87–
661 101.

662 Weishampel, D. B., P. Dodson, and H. Osmolska. 2004. The Dinosauria. University of
663 California Press, Berkley, p.1-880

664 Whitlock, J. A. 2011. Inferences of diplodocoid (Sauropoda: Dinosauria) feeding behavior
665 from snout shape and microwear analyses. PLoS One 6:e18304.

666 Wills, M. A., D. E. G. Briggs, and R. A. Fortey. 1994. Disparity as an evolutionary index: a
667 comparison of Cambrian and Recent arthropods. Paleobiology 20:93–130.

668 Young, M. T., and M. D. Larvan. 2010. Macroevolutionary trends in the skull of
669 sauropodomorph dinosaurs - the largest terrestrial animals to have ever lived. Pp.259–
670 269 *in* A. M. T. Elewa, ed. Morphometrics for Nonmorphometricians: Lecture Notes in
671 Earth Sciences. Vol. 124. Springer Berlin Heidelberg, Berlin, Heidelberg.

672 Zelditch, M. L., D. L. Swiderski, and H. D. Sheets. 2012. Geometric Morphometrics for
673 Biologists: A Primer. Academic Press, New York, p.1-488

674

675 **Author contributions**

676 PSLA, EJR and PMB conceived and developed the project idea. JM collected the data and
677 performed the analyses. JM, along with PSLA, EJR and PMB interpreted the data. All
678 authors contributed to writing the manuscript. JM designed and prepared the figures.

679

680 Figure captions

681 Figure 1. Patterns of morphospace occupation for herbivorous non-avian ornithischian and
682 sauropodomorph dinosaurs. PC1 and PC2 account for 50.4% of variation. Ornithischian and
683 sauropodomorph taxa occupy significantly different regions of shape-based morphospace ($p < 0.05$). Filled circles, Sauropodomorpha; empty circles, Ornithischia. Silhouettes represent
685 jaw profiles found in that region of morphospace.

686

687 Figure 2. Patterns of biomechanical morphospace occupation for herbivorous non-avian
688 ornithischian and sauropodomorph dinosaurs. PCo1 and PCo2 account for 25.2% of
689 variation. Ornithischian and sauropodomorph taxa occupy significantly different regions of
690 biomechanical morphospace ($p < 0.05$). Filled circles, Sauropodomorpha; empty circles,
691 Ornithischia. Silhouettes represent jaw biomechanical profiles found in that region of
692 biomechanical morphospace.

693

694 Figure 3. Patterns of biomechanical morphospace occupation for herbivorous non-avian
695 ornithischian and sauropodomorph dinosaurs. PCo1 and PCo3 account for 23.9% of
696 variation. Ornithischian and sauropodomorph taxa occupy significantly different regions of
697 biomechanical morphospace ($p < 0.05$). Filled circles, Sauropodomorpha; empty circles,
698 Ornithischia. Silhouettes represent jaw biomechanical profiles found in that region of
699 biomechanical morphospace.

700

701 Figure 4. Patterns of morphospace occupation for herbivorous non-avian dinosaurs through
702 the Mesozoic (20 Ma time bins). Based on PC1 and PC2 (accounting for 50.4% of variation).
703 Sauropodomorpha occupy isolated regions of morphospace for the majority of the Mesozoic,
704 with overlap between North American sauropods and thyreophorans between 185 and 145
705 Ma.

706

Figure 5. Patterns of biomechanical morphospace occupation for herbivorous non-avian dinosaurs through the Mesozoic (20Ma time bins). Based on PCo1 and PCo2 (accounting for 25.2% of variation). Sauropodomorphs predominantly overlap only with heterodontosaurids (202–145 Ma). Aptian–Maastrichtian marginocephalians and ornithopods occupy similar regions of morphospace (125–65 Ma).

Figure 6. Patterns of biomechanical morphospace occupation for herbivorous non-avian dinosaurs through the Mesozoic (20Ma time bins). Based on PCo1 and PCo3 (accounting for 23.9% of variation). Sauropodomorphs overlap very little with contemporaneous taxa before the latest Cretaceous (85–65 Ma). Albian–Maastrichtian marginocephalians and thyreophorans occupy similar regions of biomechanical morphospace (105–65 Ma).

Figure 7. Comparison of shape-based and biomechanical disparity curves across 10Ma time bins based on sum of variance metric. a) shape-based disparity b) biomechanical disparity. Morphological and biomechanical disparity curves are decoupled, with morphological disparity increasing through the Mesozoic and biomechanical disparity peaking in the latest Jurassic. Shaded region spans the 95% confidence intervals based on 1,000 bootstrap replicates. Disparity (dots) is plotted alongside jaw specimen sample size curve (diamonds). Flower represents earliest fossil angiosperms (Sun et al. 2002; Du and Wang 2015).

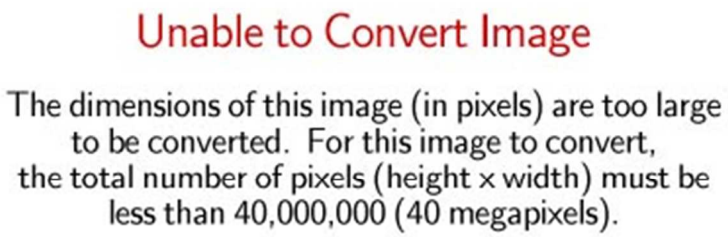

Figure 1. Patterns of morphospace occupation for herbivorous non-avian ornithischian and sauropodomorph dinosaurs. PC1 and PC2 account for 50.4% of variation. Ornithischian and sauropodomorph taxa occupy significantly different regions of shape-based morphospace ($p < 0.05$). Filled circles, Sauropodomorpha; empty circles, Ornithischia. Silhouettes represent jaw profiles found in that region of morphospace.

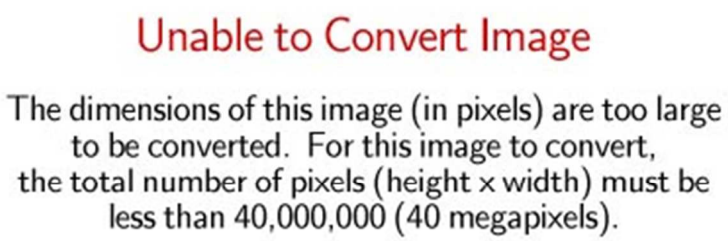

Figure 2. Patterns of biomechanical morphospace occupation for herbivorous non-avian ornithischian and sauropodomorph dinosaurs. PCo1 and PCo2 account for 25.2% of variation. Ornithischian and sauropodomorph taxa occupy significantly different regions of biomechanical morphospace ($p < 0.05$). Filled circles, Sauropodomorpha; empty circles, Ornithischia. Silhouettes represent jaw biomechanical profiles found in that region of biomechanical morphospace.

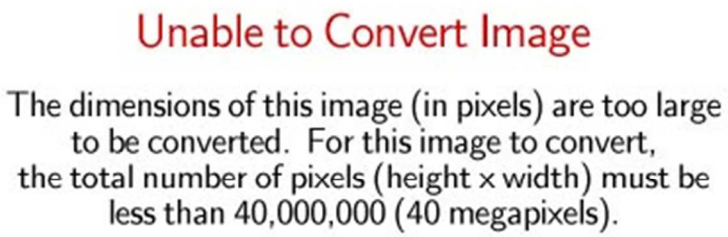

Figure 2. Patterns of biomechanical morphospace occupation for herbivorous non-avian ornithischian and sauropodomorph dinosaurs. PCo1 and PCo2 account for 25.2% of variation. Ornithischian and sauropodomorph taxa occupy significantly different regions of biomechanical morphospace ($p < 0.05$). Filled circles, Sauropodomorpha; empty circles, Ornithischia. Silhouettes represent jaw biomechanical profiles found in that region of biomechanical morphospace.

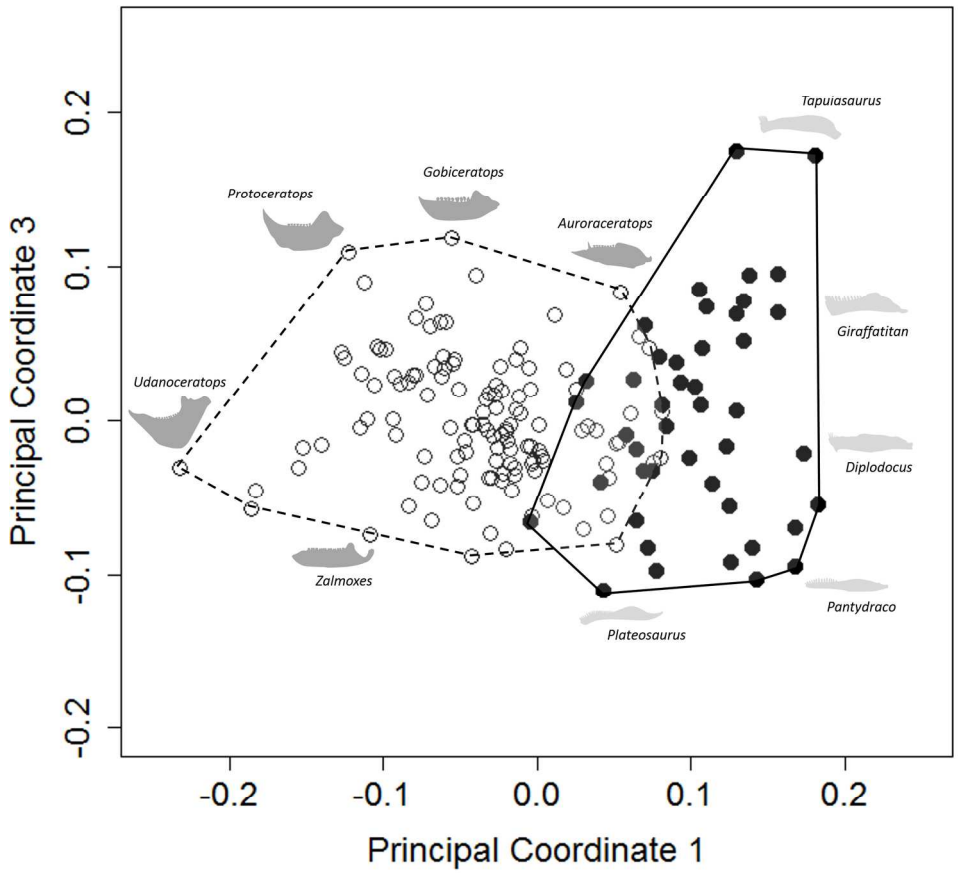

Figure 3. Patterns of biomechanical morphospace occupation for herbivorous non-avian ornithischian and sauropodomorph dinosaurs. PCo1 and PCo3 account for 23.9% of variation. Ornithischian and sauropodomorph taxa occupy significantly different regions of biomechanical morphospace ($p < 0.05$). Filled circles, Sauropodomorpha; empty circles, Ornithischia. Silhouettes represent jaw biomechanical profiles found in that region of biomechanical morphospace.

101x101mm (600 x 600 DPI)

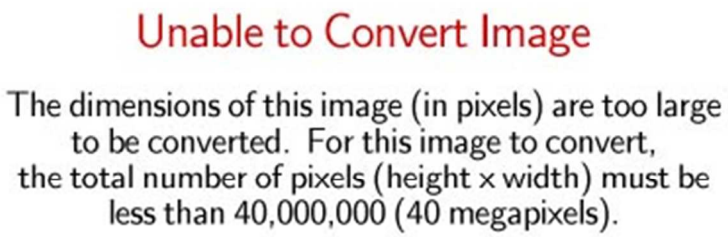

Figure 4. Patterns of morphospace occupation for herbivorous non-avian dinosaurs through the Mesozoic (20 Ma time bins). Based on PC1 and PC2 (accounting for 50.4% of variation). Sauropodomorpha occupy isolated regions of morphospace for the majority of the Mesozoic, with overlap between North American sauropods and thyreophorans between 185 and 145 Ma.

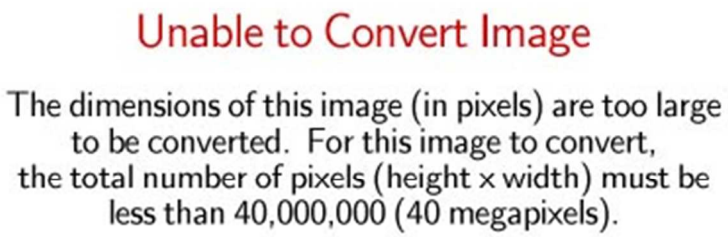

Figure 5. Patterns of biomechanical morphospace occupation for herbivorous non-avian dinosaurs through the Mesozoic (20Ma time bins). Based on PCo1 and PCo2 (accounting for 25.2% of variation). Sauropodomorphs predominantly overlap only with heterodontosaurids (202–145 Ma). Aptian–Maastrichtian marginocephalians and ornithopods occupy similar regions of morphospace (125–65 Ma).

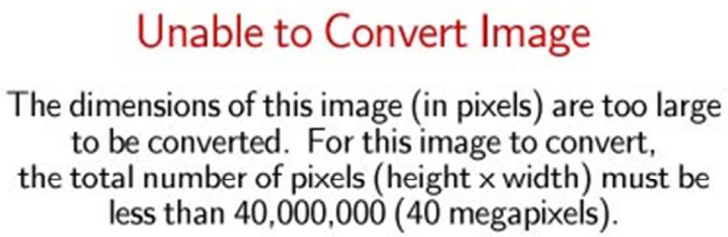

Figure 6. Patterns of biomechanical morphospace occupation for herbivorous non-avian dinosaurs through the Mesozoic (20Ma time bins). Based on PCo1 and PCo3 (accounting for 23.9% of variation). Sauropodomorphs overlap very little with contemporaneous taxa before the latest Cretaceous (85–65 Ma). Albian–Maastrichtian marginocephalians and thyreophorans occupy similar regions of biomechanical morphospace (105–65 Ma).

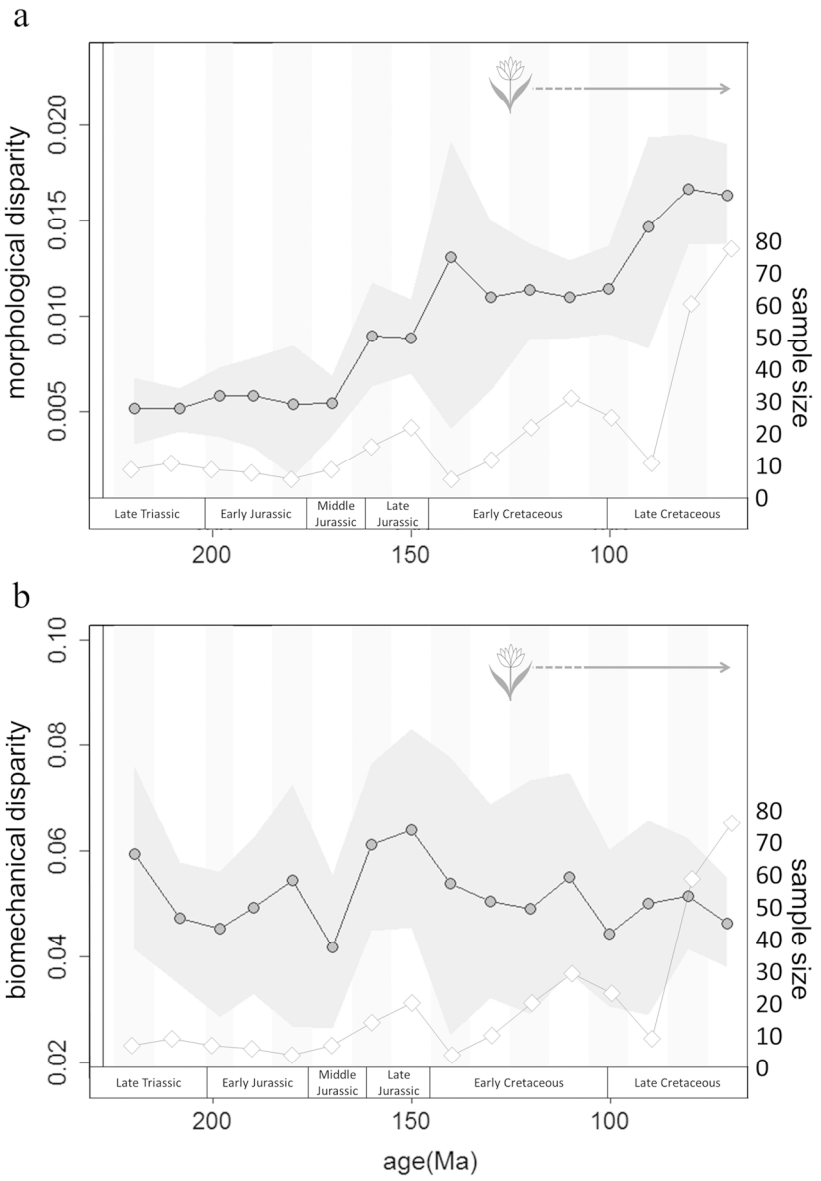

Figure 7. Comparison of shape-based and biomechanical disparity curves across 10Ma time bins based on sum of variance metric. a) shape-based disparity b) biomechanical disparity. Morphological and biomechanical disparity curves are decoupled, with morphological disparity increasing through the Mesozoic and biomechanical disparity peaking in the latest Jurassic. Shaded region spans the 95% confidence intervals based on 1,000 bootstrap replicates. Disparity (dots) is plotted alongside jaw specimen sample size curve (diamonds). Flower represents earliest fossil angiosperms (Sun et al. 2002; Du and Wang 2015).

223x326mm (600 x 600 DPI)

Table 1. Continuous biomechanical characters used in this study

Code	Functional Trait	Description
C1	Anterior Mechanical Advantage	Ratio of maximum out-lever (on functional tooth-row) and jaw muscle in-lever moment arms.
C2	Posterior Mechanical Advantage	Ratio of minimum out-lever (on functional tooth-row) and jaw muscle in-lever moment arms.
C3	Opening Mechanical Advantage	Ratio of maximum out-lever and opening in-lever moment arms.
C4	Maximum Aspect Ratio	Proxy for maximum flexural stiffness in the jaw.
C5	Average Aspect Ratio	Proxy for average flexural stiffness across the entire jaw.
C6	Relative Adductor Fossa Length	Length of adductor muscle attachment; proxy for jaw muscle size.
C7	Relative Dental Row Length	Length of functional tooth-row relative to total jaw length.
C8	Relative Articular Offset	Proxy for deviation of biting action from scissor-like mastication.
C9	Relative Mandibular Fenestra	Area of mandibular fenestrae relative to total lateral jaw area.
C10	Relative Dental Curvature	Curvature of functional toothrow; proxy for shearing vs. compressive mastication.
C11	Cheek Tooth Height : Breadth	Proxy for maximum tooth size for teeth occluding with maxillary teeth.
C12	'Premax Occ' Tooth Height : Breadth	Proxy for maximum tooth size for teeth occluding with premaxillary teeth
C13	Tooth Packing	Proxy for tooth separation and how closely teeth are packed.
C14	Predentary Tooth Procumbancy	Proxy for anterior-most tooth procumbancy.
C15	Tooth Height : Jaw Depth	Height of tooth present above deepest section of functional jaw taken.
C16	Relative Symphyseal Length	Proxy for robustness of anterior jaw.
C17	Mandibular Symphysis Orientation	Proxy for symphyseal resistance to bending during biting.
C18	Predentary Offset	Proxy for predentary curvature in ornithischians.

Table 2. Results of significance testing (NPMANOVA) on morphospace occupation (PC1 and PC2) and biomechanical occupation (PCo1 and PCo2; PCo1 and PCo3) between Ornithischia and Sauropodomorpha (at $p<0.05$)

Shape–based Morphospace	Sauropodomorpha	Ornithischia
Sauropodomorpha	-	**<0.001**
Ornithischia	**<0.001**	-

Biomechanical Morphospace	Sauropodomorpha	Ornithischia
Sauropodomorpha	-	**<0.001**
Ornithischia	**<0.001**	-

Table 3. NPMANOVA significance testing between clade occupations of biomechanical morphospace through time. Bold p-values represent significant differences (at $p<0.05$).

Time Bin	NPMANOVA p-values					
225–202Ma	Clades	SA	BO			
	SA	-	0.114			
	BO	0.114	-			
202–185Ma	Clades	SA	BO			
	SA	-	**0.009**			
	BO	**0.009**	-			
185–165Ma	Clades	SA	BO	TH		
	SA	-	0.142	1		
	BO	0.142	-	1		
	TH	1	1	-		
165–145Ma	Clades	SA	BO	TH	OR	MA
	SA	-	0.505	**0.009**	**0.015**	1
	BO	0.505	-	0.520	0.124	1
	TH	**0.009**	0.520	-	0.158	1
	OR	**0.015**	0.124	0.158	-	1
145–125Ma	Clades	SA	OR	MA		
	SA	-	0.084	**0.003**		
	OR	0.084	-	**0.016**		
	MA	**0.003**	**0.016**	-		
125–105Ma	Clades	SA	TH	OR	MA	
	SA	-	0.186	**<0.001**	**<0.001**	
	TH	0.186	-	**0.003**	**0.007**	
	OR	**<0.001**	**0.003**	-	**<0.001**	
	MA	**<0.001**	**0.007**	**<0.001**	-	
105–85Ma	Clades	SA	TH	OR	MA	
	SA	-	0.164	**0.002**	**0.043**	
	TH	0.164	-	**0.005**	**0.037**	
	OR	**0.002**	**0.005**	-	**<0.001**	
	MA	**0.043**	**0.037**	**<0.001**	-	
85–65Ma	Clades	SA	TH	OR	MA	
	SA	-	**<0.001**	**<0.001**	**<0.001**	
	TH	**<0.001**	-	**<0.001**	**<0.001**	
	OR	**<0.001**	**<0.001**	-	**<0.001**	
	MA	**<0.001**	**<0.001**	**<0.001**	-	

SA = Sauropodomorpha; BO = Basal Ornithischia; TH = Thyreophora; OR = Ornithopoda; MA = Marginocephalia